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Foliar turnover rates in Finland — comparing estimates from needle-cohort and litterfall-biomass methods

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Soil carbon models serving national greenhouse gas (GHG) inventories need precise litter input estimates that typically originate from regionally-averaged and species-specific biomass turnover rates. We compared the foliar turnover rates estimated from long-term measurements by two methods: the needle-cohort based turnover rates (NT; 1064 Scots pine and Norway spruce stands), used in Finnish GHG inventory, and litterfall-biomass based turnover rates (LT; 40 Scots pine, Norway spruce, and silver and downy birch stands). For evergreens, regionally averaged NT values (± SD) (0.139 ± 0.01, 0.1 ± 0.009 for spruce south and north of 64°N, and 0.278 ± 0.016, 0.213 ± 0.028 for pine, respectively) were greater than those used in the GHG inventory model in Finland (0.1, 0.05 for spruce in the south and north, and 0.245, 0.154 for pine, respectively). For deciduous forests, averaged LT values ± SD (0.784 ± 0.162, 0.634 ± 0.093 for birch in the south and north) were close to that (0.79) currently used for the whole of Finland.

Introduction

Boreal forest soils contain large carbon stocks in a dynamic state driven by continuously changing gains and losses (Rapalee *et al*. 1998). The long-term difference between litterfall inputs from the current vegetation and the soil carbon outputs from decomposers and leaching can be imbalanced by e.g. warming of boreal climate (Tietäväinen *et al*. 2010). Such imbalance, i.e. when drivers of the litterfall inputs or soil carbon pools are changing from the long-term state, is raising a key question in climate change mitigation, whether soils continue to accumulate carbon or become a source of carbon to the atmosphere in the long-term (Kirschbaum 2000). Estimates of the soil carbon stock change are needed for the national level greenhouse gas inventories, and are called upon by the Kyoto protocol and Uniated Nations Framework Convention on Climate Change (UNFCCC) (DeLuca and Boisvenue 2012). Changes in soil carbon stocks are commonly estimated with soil carbon models such as CENTURY, ROMUL or Yasso07. Accurate estimation of carbon stock changes put emphasis on the quality of both litterfall inputs and decomposition data (Palosuo *et al*. 2012). For example, the uncertainties of Yasso7 parameter values of

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decomposition were reduced to around 2% in tundra when extensive litterbag data was used for fitting (Tuomi *et al*. 2009).

The litterfall production rates are generally highly uncertain, which may still lead to underestimating or overestimating soil carbon stock changes (Ortiz *et al*. 2013). Ortiz *et al*. (2013) also demonstrated that climate variability is important contributor to soil organic carbon changes. Therefore, disregarding the effect of climate gradient on mean litter input rates may lead to biased soil carbon stock change estimates both at the national and regional levels.

The litter input in soil carbon models is commonly defined as a proportion of the estimated stand foliar biomass, also called the biomass turnover rate. In soil carbon modelling for the Finnish greenhouse gas inventory, the foliar biomass turnover rates for evergreens are based on an inverse number of needle cohorts of trees (proportion of needles shed annually) corrected for the weight loss before shedding, while foliar turnover rates for deciduous are based solely on the foliar mass loss (resorption) during the yellowing process in autumn as the whole leaf mass is shed every year (Muukkonen and Lehtonen 2004, Muukkonen 2005, Starr *et al*. 2005, Liski *et al*. 2006, Ministry of the Environment 2013). The foliar biomass turnover rates that are used in the Finnish model for annual greenhouse gas (GHG) inventory are averaged for the large regions of southern and northern Finland for coniferous species, and for the whole country for deciduous.

The latitudinal variation of number of needle cohorts is well known, and needle litterfall levels of coniferous species vary depending on climatic factors (Starr *et al*. 2005, Saarsalmi *et al*. 2007). Also, for deciduous species foliar turnover varies depending on different resorption patterns related to species and climate (Hagen-Thorn *et al*. 2006, Nordell and Karlsson 1995). Given the spatial variation of the number of needle cohorts and resorption patterns, there is a need to compare the needle-cohort based turnover rates (NT) with alternative methods. One option is a ratio between the measured foliar litterfall and modelled foliar biomass (e.g. Ågren *et al*. 2009) which we call the litterfall-biomass turnover rate (LT).

In this study, we evaluated foliar turnover rates derived from the needle-cohort method (NT) with those based on litterfall-biomass method (LT). Additionally, we aimed to downscale currently used regional NT estimates to more localized NT estimates in order to account more precisely for the spatial variation in litter fall. For pine (*Pinus sylvestris*) and spruce (*Picea abies*) sites throughout Finland we compared the NT derived from large dataset of needle-cohort measurements with LT based on long-term litterfall and stand measurements. For birch (*Betula pendula* and *Betula pubescens*) sites across Finland, we estimated foliar litterfall-biomass turnover rates from the proportion of leaf mass remaining following resorption during autumnal leaf senescence. Both the NT and LT estimates of foliar turnover rates were then compared with the default rates used in the Finnish GHG inventory model.

We first quantified the annual sums of litterfall across Finland. For litterfall-biomass ratios, we developed new birch foliar biomass models based on published values of foliage of harvested birch trees (Ilomäki *et al*. 2003, Parviainen 1999, Repola 2008). For pine and spruce, we used two existing foliar biomass models (Marklund 1988, Repola 2009). Secondly, we compiled data on needle cohorts for sites across Finland and applied measurements of proportion of foliar mass remaining following resorption to generate NT estimates for each site. We produced a modelled spatial NT estimate for entire Finland. Thirdly, we present a comparison between the mean LT values of stands with litterfall measurements and the modelled NT values and we evaluate birch LT values by separately evaluating the performance of our biomass models and the estimated autumnal resorption. Finally, we discuss the reasons behind differences in the turnover rate estimates between methods, and also between our estimates and current foliar turnover rates used in the Finnish GHG inventory model.

Material and methods

Litterfall-biomass derived foliar turnover rates

The foliar litterfall-biomass turnover rates (LT)

were estimated as ratios between measured foliar litterfall and modelled foliar biomass (both in kg m^{-2} y^{-1}). Foliar litterfall and stand data were collected from 15 Scots pine, 13 Norway spruce, and 12 Silver and downy birch dominated sites distributed across Finland (Fig. 1 and Appendix 1). The data came from the long-term seed-crop monitoring sites (e.g. Kouki and Hokkanen 1992, Pukkala *et al*. 2010) and from the ICP intensive forest sites (Ukonmaanaho *et al*. 2008). Stands with litterfall data represented well the current state of Finnish forests in terms of fertility classes, but in terms of stand age the older age classes were overrepresented. Litterfall time series of seed-crop sites were collected by Finnish Forest Research Institute (Metla) during the period between 1960 and 2010 (Fig. 2). Litterfall time series of ICP forest sites were also collected by Metla as part of the International Co-operative Program on the Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) between 1996 and 2011 (Fig. 2). ICP forest sites were established in addition to seed-crop monitoring sites and both were the networks of plots with litterfall measurements.

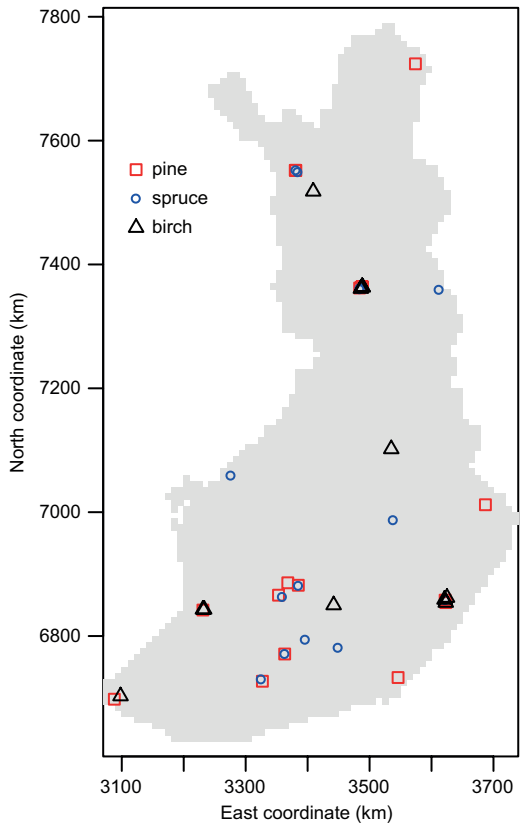

Fig. 1. Locations of the ICP intensive forest and Seed-crop sites at which foliar litterfall of Scots pine, Norway spruce, and silver and downy birch were measured. The spatial position of each site is given as N and E coordinates (km) in the Finnish KKJ-3 (YKJ) coordinate system used with zone 3 countrywide (YKJ). The Finnish KKJ-3 (YKJ) is based on the European Datum 1950 (ED50) coordinate system.

Litterfall and tree stands measurements

On each plot, litterfall was collected into a meshed cotton bag attached at the bottom of a funnel-shaped litter trap that had a collecting surface area of 0.5 m^2 and was installed 1.5 m above-ground. Approximately 36% of the seed-crop data, mainly before the 1980s, was collected by litter traps with surface areas of 0.05 m^2. For birch seed-crop sites, litterfall was collected by funnel-shaped litter traps with a surface area of 0.05 m^2 which were installed 1.0 m above-ground. Twelve litter traps were used at ICP sites while the number at seed-crop sites varied from 10 to 15.

At all sites, the litter traps were emptied at least once a month during a snow-free period. Littefall was separated into foliage and other litter (i.e. twigs). The first collection after the snowmelt comprised the accumulated litterfall over winter (snow on the ground). The dates of collections varied between the years and plots. Therefore, we only accepted annual sums of litterfall measurements with the annual collection period of more than 320 days. The collection year followed an approximated annual phenological litterfall cycle rather than a calendar year. To ensure the comparability of annual sums among plots, we predefined the start and end of the collection periods. For pine and spruce, we set the collection year's beginning on day of calendar year (DoY) 200 and collection year end on DoY 199 next year. The birch collection year began on DoY 150 and ended on DoY 149 next year. The foliar litterfall was a sum of green and brown foliage collected into the litter trap, air-dried and weighed to the nearest 1 mg (seed-crop data) or 0.1 mg (ICP data).

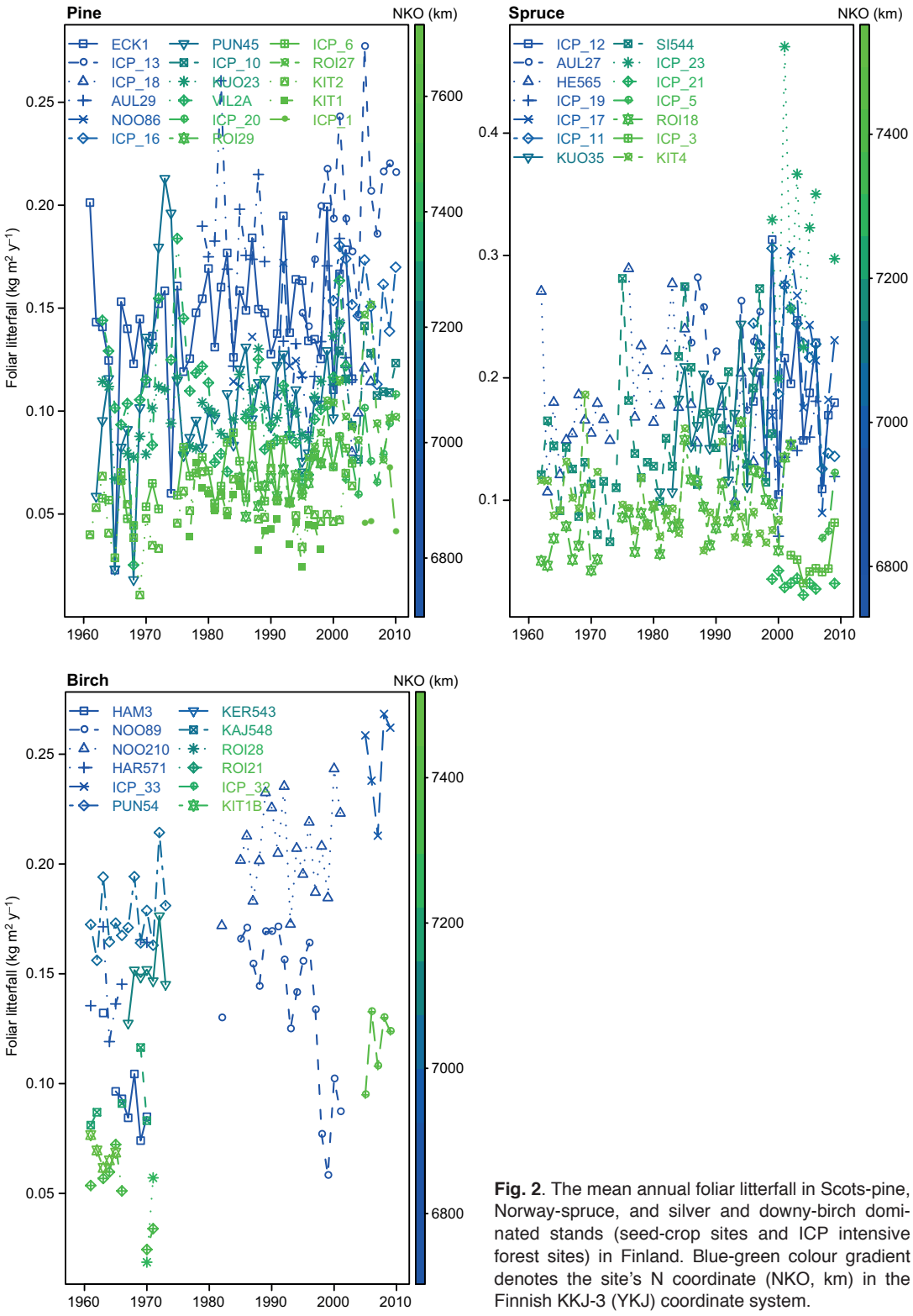

Fig. 2. The mean annual foliar litterfall in Scots-pine, Norway-spruce, and silver and downy-birch dominated stands (seed-crop sites and ICP intensive forest sites) in Finland. Blue-green colour gradient denotes the site's N coordinate (NKO, km) in the Finnish KKJ-3 (YKJ) coordinate system.

The average annual foliar litterfall was 0.103 kg m^{-2} y^{-1} for pine-dominated forests, and 0.147 and 0.146 kg m^{-2} y^{-1} for spruce- and birch-dominated forests (Fig. 2). The largest range of the annual litterfall values between northern and southern Finland was found among the spruce stands (0.022 to 0.471 kg m^{-2} y^{-1}), while the lowest among the birch stands (0.187 to 0.268 kg m^{-2} y^{-1}).

The stand data were collected from both the seed-crop and ICP litter fall plots of mainly 900 m^2 (ICP) or 2000 m^2 (seed-crop) during the litterfall collection periods (Appendix 1). Breast-height diameter (D_{13}) and height (H) of all trees were measured. The crown ratio (CR), which is the ratio between H and height of the lowest living branch, was monitored only for the ICP trees and seed-crop evergreens, whereas for the seed-crop birch, CR was mainly missing (Appendix 1). The seed-crop stands (age 119, years, median 122) were older than the ICP stands (age 102 years, median 85). The average diameter and height of the pine and spruce stands were somewhat similar: D_{13} = 25 cm and H = 19 m (*see* Appendix 1). However, the spruce stands were on average more stocked with a larger basal area (26 m^2 ha^{-1}) than the less-dense pine stands, with a basal area of 21 m^2 ha^{-1}. The spruce crowns were on average 20% longer than pine crowns, and both species showed slight crown prolongation tendency from south to north. Number of trees was higher in birch than spruce stands and, as a result, birch trees were more slender than spruce trees, with mean D_{13} = 17 cm, mean H = 17 m, and mean basal area of only 14 m^2 ha^{-1}.

Tree stand data were collected either every 5 years from ICP intensive forest sites but only once or twice from seed-crop sites. To increase the number of litterfall/biomass data, we used the matching years between the litterfall and tree measurements plus one year prior and one year after the year of tree stand measurements. Plots where stand was measured multiple times were used only once, but the standard error of the litterfall-biomass turnover rate was reduced if more foliage biomass and litterfall years matched. Thus the mean turnover rate represented the ratio between the mean of litterfall and the mean of biomass for matching years between both data sets.

Foliar biomass modelling of pine and spruce

Pine and spruce foliar biomass were estimated tree-wise by using Repola's (2009) A4 and A10 and Marklund's (1988) T18, T19, G16 and G17 foliar biomass equations (Appendix 2). Repola's (2009) models require breast height diameter (D_{13}), height (H), and crown length. Marklund's (1988) models for spruce were based on D_{13}, H, and crown length, whereas Marklund's models for pine foliar biomass require D_{13}, H, crown length, and north (N) coordinate (100 km). Foliage was modelled up to 2 years prior and 2 years after the year of measurement of each tree.

Foliar biomass modelling of birch

The foliar biomass of birch was first estimated by using Repola's (2008) foliar biomass equations. However, Repola's (2008) models were built using a small sample of trees (21) from southern Finland. Therefore, we built new birch foliage biomass models based on an extended dataset of harvested birch foliar biomass data (Appendix 3) from 12 trees of Parviainen (1999), 18 trees of Ilomäki *et al*. (2003), and 21 trees of Repola (2008). In spite of extending the dataset to all available sources, the spatial extent of harvested trees was still relatively small. Therefore, we built models both including and excluding latitude as a predictor. We also built models including and excluding crown ratio (crown length to height ratio), because of the character of our tree measurements (crown length was not available for older sites). We expected birch foliar biomass of individual trees of the studies by Parviainen (1999), Ilomäki *et al*. (2003), and Repola (2008) to be spatially correlated. Therefore, to avoid bias towards locations with more trees, we assigned a spatial position for each tree based on the coordinates of each subplot of each study and an approximate distribution of trees inside subplots.

Firstly, the models predict the foliar biomass with diameter and crown ratio using the following equations:

$$\ln\left(y_{k,i}\right) = \beta_0 + \beta_1 \frac{d_{sk,i}}{\left(d_{sk,i} + 8.37\right)} + \beta_2 \mathrm{cr}_{k,i} + \varepsilon, \qquad (1a)$$

$$\ln\left(y_{k,i}\right) = \beta_0 + \beta_1 \frac{d_{sk,i}}{\left(d_{sk,i} + 8.37\right)} + \beta_2 \mathrm{cr}_{k,i} + \beta_3 \frac{\mathrm{NKO}_{k,i}}{1000} + \varepsilon, \quad (1b)$$

where $y_{k,i}$ is the foliar biomass (kg m^{-2} y^{-1}) of kth stand and ith tree, $d_{sk,i}$ (cm) is the stump diameter [d_s (cm) = $1.25D_{13}$ + 2; Laasasenaho (1982) as cited in Repola (2008)] transformed with the constant 8.37 searched iteratively by choosing the transformation producing the lowest residual standard error, $\mathrm{cr}_{k,i}$ is the crown ratio, β_0, β_1 and β_2 are coefficients of the linear regression (Table 1), $\mathrm{NKO}_{k,i}$ (km) is N coordinate (km) in the Finnish KKJ-3 (YKJ) coordinate system used with zone 3 countrywide (YKJ) which is based on the European Datum 1950 (ED50) coordinate system, and ε is the residual error.

Secondly, the models predicted birch foliar biomass with diameter and slenderness as follows:

$$\ln\left(y_{k,i}\right) = \beta_0 + \beta_1 \frac{d_{sk,i}}{\left(d_{sk,i} + 5.12\right)} + \beta_2 h_{\mathrm{dk},i} + \varepsilon, \quad (2)$$

where $y_{k,i}$, $d_{sk,i}$, β_0, β_1 and β_2, ε are explained above, and $h_{\mathrm{dk},i}$ is the slenderness [$h_d = H/(d_s \times 100)$], Ilomäki *et al*. 2003).

We avoided bias from the spatial correlation for each foliar biomass model by calculating differential weights for each tree by a variogram model (e.g. Webster and Oliver 2001, Räty *et al*. 2011). Firstly, we calculated pair-wise distances between all trees $h_{i,j} = \|s_i - s_j\|$ (where s_i and s_j are the positions of two trees). Secondly, we estimated an empirical variogram 2γ of the variance in the residual (ε) at lag classes (lags) defined by boundaries h_k (km) = 0.03, 0.1, 2, 71, 132, 141, 182, and 195 (Fig. 3) using the equation:

$$2\hat{\gamma}\left(h_k\right) = \frac{1}{\left|N\left(h_k\right)\right|} \sum_{i,j \in N(h_k)} \left[\varepsilon\left(s_i\right) - \varepsilon\left(sj\right)\right]^2, \quad (3)$$

where $\hat{\gamma}()$ is the semi-variogram, $N(h_k)$ is the set of pairs of trees with $h_{ij} \in h_k$, and $|N(h_k)|$ is a size of the set. Thirdly, we fitted a Gaussian function to the empirical variogram allowing a non-zero value at distance zero (nugget), the approachable maximum of the variogram (sill), and the range between nugget and sill (partial sill) (Fig. 3). The fitted variogram showed a steep increase in semi-variance at distances below 2 km (between trees of individual studies) with saturation at longer distances (between studies) (Fig. 3). Finally, we determined the weights for refitting each foliar biomass model by summing the rows of the inverse of covariance matrix with a diagonal set to the sill value. Trees in larger clusters typically received smaller weights. Beside avoiding bias towards the location of more trees by using differential weights, also the residual standard errors of biomass models were lowered from 0.24 to 0.06 (Eqs. 1a and b) and from 0.31 to 0.14 (Eq. 2). The smallest root mean squared error (RMSE) among three birch models was the model that included slenderness (Fig. 4 and Table 1). All data analysis was done using the R software for statistical computing and graphics (R Core Team 2013). First, we used functions of the *nlme* package of R (Pinheiro *et al*. 2013) for fitting nonlinear models without weights. Subsequently, we fitted the same models with weights determined from universal kriging while using the *gstat* package of R (Bivand *et al*. 2008). We used functions of

Table 1. Parameter estimates and their standard errors for the coefficients of the birch foliar biomass models corrected for spatial correlation of trees by universal kriging. Birch foliar biomass is a function of the stump diameter, crown ratio $f(d_s,\mathrm{cr})$ (Eq. 1a), and N coordinate $f(d_s,\mathrm{cr},\mathrm{NKO})$ (Eq. 1b) or as function of transformed stump diameter and slenderness $f(d_s,h_d)$ (Eq. 2). The SE values of the parameters are probably underestimated, because they do not account for spatial correlations in the tree residuals. d_s = stump diameter (cm), cr = crown ratio, NKO = N coordinate (km) in the Finnish KKJ-3 (YKJ) coordinate system, h_d = slendernes

Foliar Biomass model	β_0 ± SE	β_1 ± SE	β_2 ± SE	β_3 ± SE	RMSE
Eq. 1a: $f(d_s,\mathrm{cr})$	–7.832 ± 0.22	10.043 ± 0.255	2.875 ± 0.198		1.059
Eq. 1b: $f(d_s,\mathrm{cr},\mathrm{NKO})$	–4.355[a] ± 6.212	10.034 ± 0.257	2.834 ± 0.213	–0.500[b] ± 0.895	1.041
Eq. 2: $f(d_s,h_d)$	–4.656 ± 0.394	9.589 ± 0.396	–0.024 ± 0.002		1.012

[a] $p = 0.48$, [b] $p = 0.58$, for other coefficients $p < 0.001$.

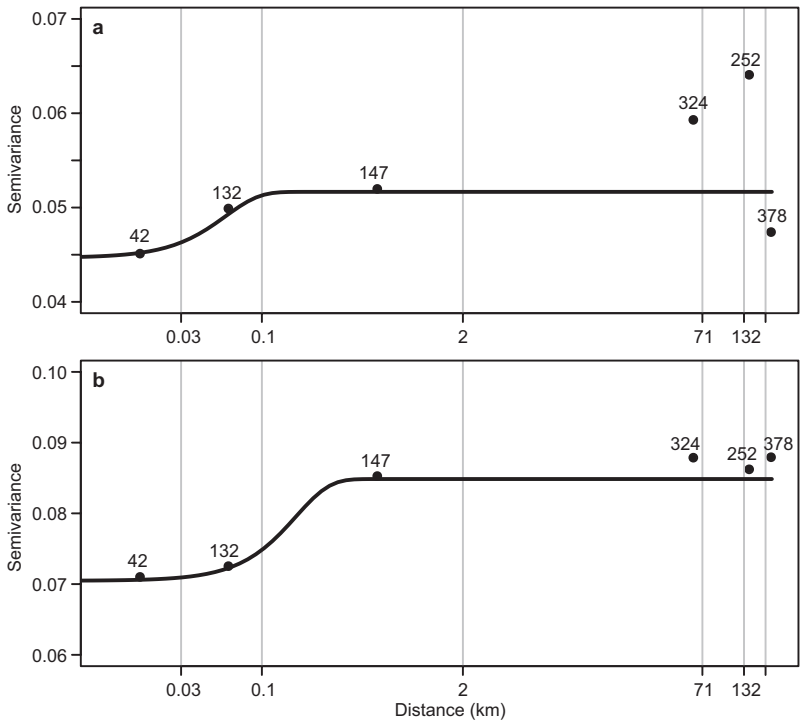

Fig. 3. Empirical semivariograms of the birch foliar biomass models (**a**) Eq. 1a and (**b**) Eq. 2 for the predetermined distance classes (grey vertical lines) fitted with the Gaussian function. Birch foliar biomass is a function of the stump diameter and crown ratio $f(d_s, \mathrm{cr})$ (Eq. 1a) or a function of stump diameter and slenderness $f(d_s, h_d)$ (Eq. 2). Dots show the semi-variance for the indicated number of pairs in the predetermined distance class, and the black line is the fitted function. d_s is the stump diameter, cr is the crown ratio, and h_d is the slenderness

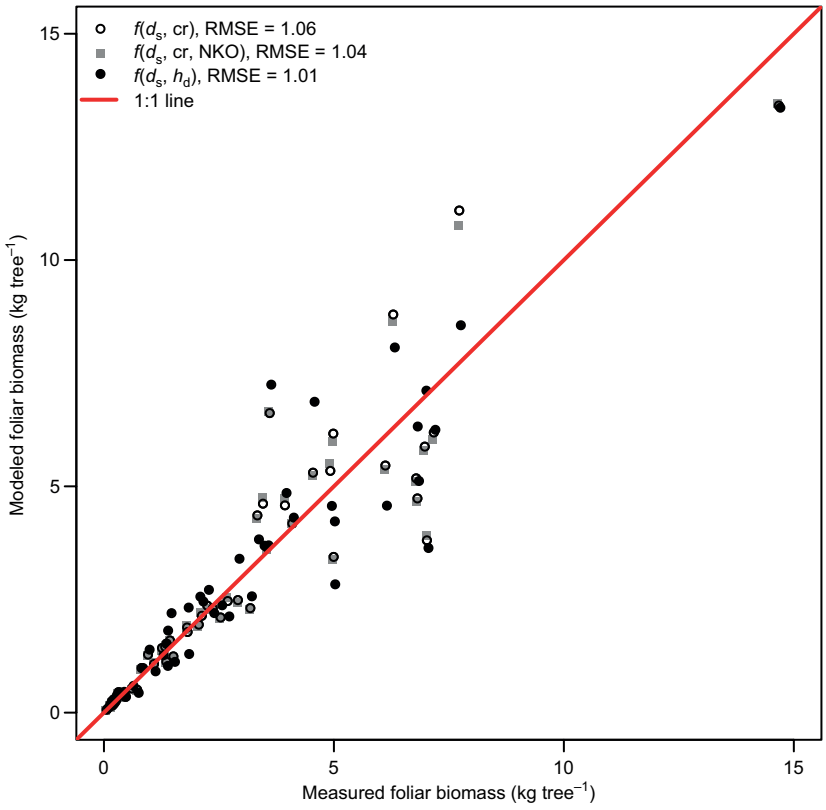

Fig. 4. Birch foliar biomass from compiled dataset of harvested trees (Parviainen 1999, Ilomäki *et al.* 2003, Repola 2008; *see* Appendix 3), and modelled as a function of the stump diameter, crown ratio $f(d_s, \mathrm{cr})$ (Eq. 1a) and N coordinate $f(d_s, \mathrm{cr}, \mathrm{NKO})$ (Eq. 1b), or as a function of stump diameter and slenderness $f(d_s, h_d)$ (Eq. 2). Birch foliar biomass models were corrected for spatial correlation between the trees. d_s is the stump diameter (cm), cr is the crown ratio, NKO is the N coordinate (km) in the Finnish KKJ-3 (YKJ) coordinate system, and h_d is the slendernes.

stats package of R for testing the significance in observed trends by fitting a one way analysis of variance model, and for testing significant differences between the groups of data by performing Welch's two sample *t*-test after checking visually distributions for normality.

To evaluate the effect of using different biomass models on the turnover rates in relation to N coordinate, we fitted linear regression models to turnover rates of species-specific models [Repola's A4 and A10, Marklund's T19, G17, T18, and G16 (*see* Appendix 2)]. Fits were weighted by annual litterfall at each site. We compared the r^2 values of fits and relative slopes of the fits. The relative slope is the slope of the fit multiplied by 1000 and divided by the mean modelled foliar biomass or mean basal area. We did not fit regression lines for turnover rates derived with birch models, because of high uncertainty in the model of stump diameter and slenderness $f(d_s,h_d)$, and lack of data for the more precise models with stump diameter and crown ratio $f(d_s,\mathrm{cr})$, and N coordinate $f(d_s,\mathrm{cr},\mathrm{NKO})$.

Needle-cohort-derived foliar turnover rates

The annual needle-cohort assessment was done on 625 Scots pine plots and 439 Norway spruce plots, constituting 8200 Scots pines and 4757 Norway spruces. The plots are part of the ICP extensive monitoring plot data and do not include litterfall measurements; *see* e.g. (Nevalainen *et al*. 2010a). Measurements on plots were made between 1986 and 2006, but most of the needle cohort time series originated from the period 1995–2006. Basic tree measurements, including height and diameter, were also made at all plots in the control survey. The age of stands was normally distributed and the whole country average was 62 years for pine and 72 years for spruce. Stands were younger in the south and older in the north. The average diameter and height of pine and spruce stands slightly differed: spruces were larger (D_{13} = 18 cm and H = 14 m) than pines (D_{13} = 16 cm and H = 10 m). Distribution of fertility and age classes of the stands with needle-cohort observations represented well the current state of Finnish forests.

Needle-cohort quantities of individual trees were monitored on each plot annually during July–August by trained observers. Sets of needle cohorts were observed on branches located in the lower canopy of dominant trees using binoculars. The needle cohort was counted as a whole even if the amount of defoliated needles reached 50%. The needle-cohort records from the lower canopy were used as they were easier to measure than cohort quantities from the top canopy. A minimum of 20 trees were monitored per southern plot, and a minimum of 10 trees per northern plot.

For each tree, needle biomass was predicted using measured diameter (D_{13}) and Marklund's (1988) models. Modelled needle biomass was used to assign weight for each tree when averaging the number of needle cohorts of all trees on the given plot. Mean number of needle cohorts differed between Scots pine and Norway spruce plots, and for both species increased with latitude (Fig. 5). Pine cohort quantities ranged from 1 (only on 3 sites) in the south to 5.5 in the north, whereas for spruce, the number of needle cohorts extended from 4 to 14, respectively.

The large scale spatial variation of needle turnover rates were estimated from the ICP extensive monitoring plot data. We estimated needle turnover rates to be an inverse of the number of needle cohorts. In order to generalise the needle turnover rates across Finland, universal kriging methods were applied using the *gstat* package of R (Bivand *et al*. 2008). The general universal kriging model is:

$$U(s_{i0}) = \mu(s_i) + \delta(s_i), \quad (4)$$

where $U(s_{i0})$ is a random variable representing the inverse of needle-cohort count (an approximation for needle turnover rate) at location s for the ith species, $\mu(s_i)$ represents the large-scale trend and $\delta(s_i)$ is a stationary random process. The applied trend functions for needle turnover rates at Scots pine and Norway spruce sites were:

$$\mu(s_{\mathrm{pine}}) = \zeta_0 + \zeta_1 x_1^2 + \zeta_3 x_2, \quad (5)$$

$$\mu(s_{\mathrm{spruce}}) = \zeta_0 + \zeta_1 x_1, \quad (6)$$

where x_1 is the Finnish KKJ-3 (YKJ) N coor-

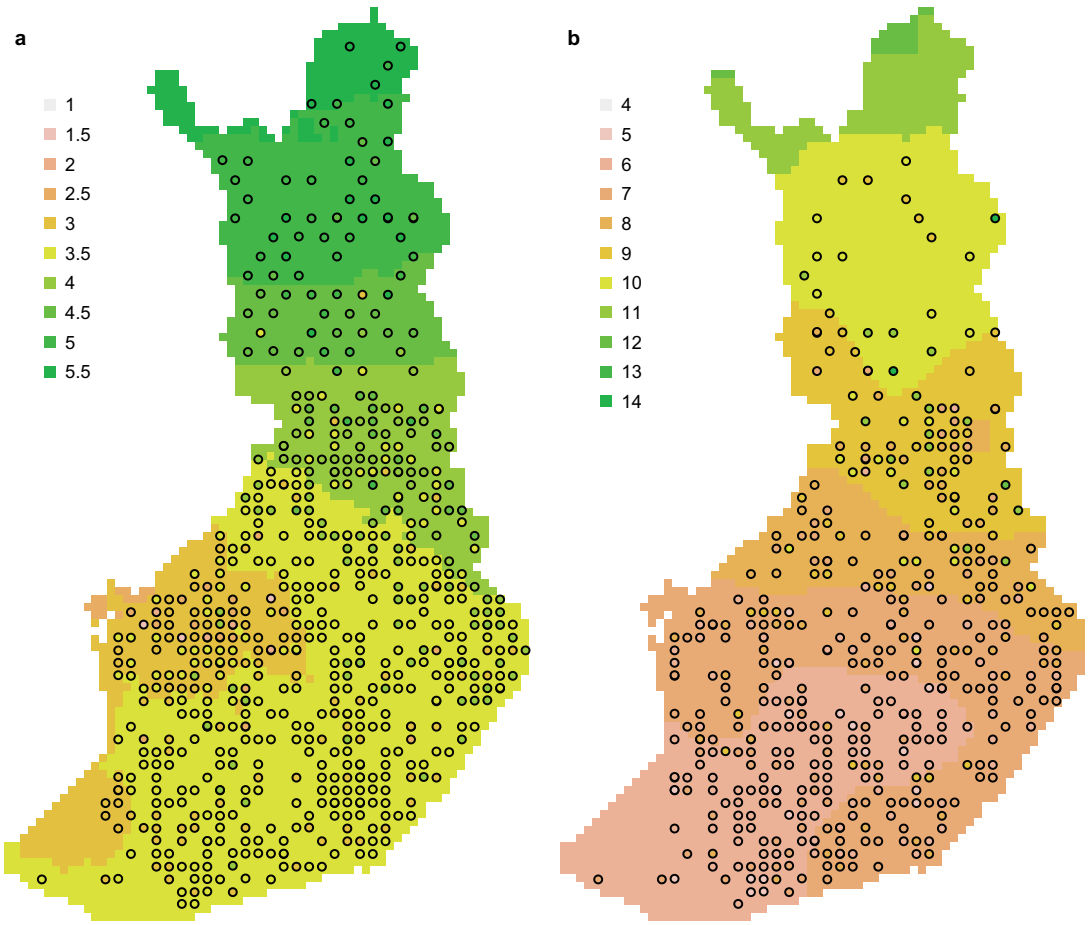

Fig. 5. Mean number of needle cohorts in (**a**) Scots-pine and (**b**) Norway-spruce stands in Finland. For each ICP extensive monitoring plot (circles), the measured number of needle cohorts is overlaid on top of the spatial estimate of the number of needle cohorts modelled by the universal kriging model. To download the estimated number of needle cohorts for the grid based maps visit www.metla.fi/ghg/improving-soil-carbon-estimation.htm.

dinate (km), and x_2 is the mean precipitation during the period 1971–2000 at location s, with ζ_0, ζ_1 and ζ_2 indicating coefficients of the linear trend (Table 2). The fitted variogram showed a gradual increase in semi-variance with distance and stronger autocorrelation between neighbouring trees for Norway spruce than for Scots pine (Fig. 6). The universal kriging model was then used to predict needle turnover rates for Finland. Turnover rates derived from the spatial

Table 2. Parameter estimates and their standard errors for the coefficients of the production rate model of foliar litterfall based on needle cohorts (NC) corrected by universal kriging. The Scots pine needle-cohort turnover rate (Eq. 5) is a function of N coordinate in the Finnish KKJ-3 (YKJ) coordinate system (NKO, km) and mean annual precipitation (prec, mm). The Norway spruce needle-cohort turnover rate (Eq. 6) is a function of NKO.

NC model	$\zeta_0 \pm$ SE	$\zeta_1 \pm$ SE	$\zeta_2 \pm$ SE
Eq. 5: *f*(NKO,prec)	0.727 ± 0.115	–9.00e–09 ± 2.00e–09	–8.14e–05 ± 4.48e–05
Eq. 6; *f*(NKO)	0.646 ± 0.052	–7.39e–05 ± 7.44e–06	

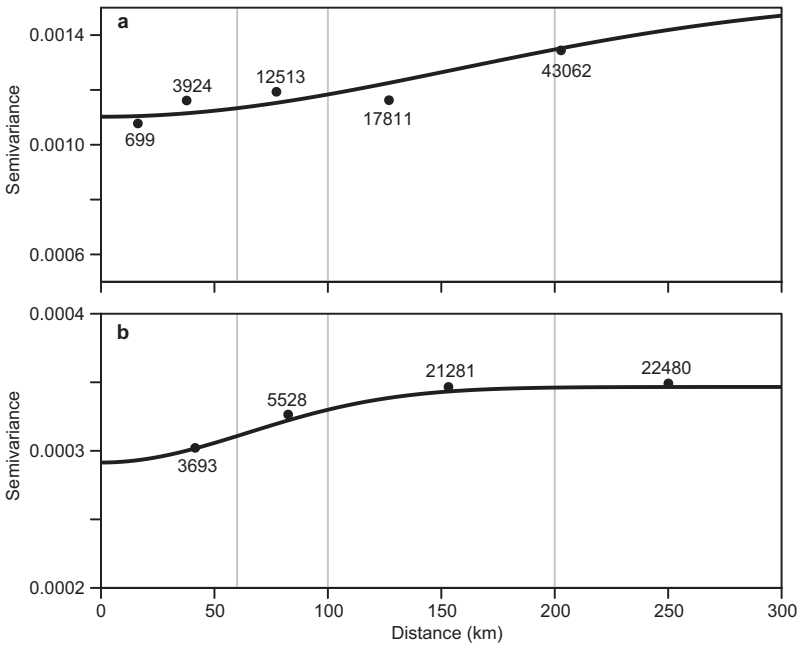

Fig. 6. Empirical semivariograms of the universal kriging models for (**a**) Scots pine and (**b**) Norway spruce based on the number of needle cohorts for the given distances (km) fitted with the Gaussian function. Dots show the semi-variance in the distance class, and the black line is the fitted function.

kriging model were based on spatial interpolation of residuals from the model based on N coordinate and mean precipitation for pine (Eq. 5) and residuals from the model based on N coordinate in case of spruce (Eq. 6). This combined approach of linear models and spatial interpolation of residuals enabled considering the effect of "climate" (indirectly expressed as N coordinate) and local differences by giving more weight to areas with more plots (Fig. 6). The use of N coordinate in the model enabled spatial extrapolation of prediction into the areas with sparse plots (north). Turnover rates estimated by the spatial kriging model were evaluated against the litterfall-biomass ratios for the locations of stands with litterfall measurements (seed-crop plots, ICP intensive plots).

The mean precipitation values for 1971–2000 were estimated from the Finnish Meteorological Institutes (FMI) 10×10 km grid (Venäläinen *et al*. 2005). The estimation was made for the National Forest Inventory (NFI) 10 grid (Korhonen *et al*. 2006) and also for the litter trap sites used in this study. The weather data from the closest grid point were allocated to each NFI 10 plot and also to each litter trap site. Thereafter, the kriging model was applied separately for Scots pine and for Norway spruce to obtain predictions.

Resorption of mass associated with senescence

Resorption correction of needle-cohort derived foliar turnover rates

In order to account for the effects of nutrient and carbohydrate resorption on the total biomass of shed foliage, the predicted inverse of needle-cohort counts $U(s_0)$ was corrected with the species-specific fraction of weight remaining after the resorption accordingly:

$$U_{r(s_0)} = U_{(s_0)} \frac{w_b}{w_g}, \quad (7)$$

where W_b is the weight of foliar litterfall (brown) and W_g is the weight of sampled foliage (green). The W_b/W_g ratios were averaged for the whole country for each species before applying the resorption correction of cohort turnover rates.

The species-specific weight loss coefficients (W_s, %) were calculated from ICP sites as follows:

$$w_s = \left(1 - \frac{w_b}{w_g}\right) \times 100, \quad (8)$$

Sampling of needles was done according to Rautio *et al*. (2010). The sampled needles were taken from the lower part of the upper third of the

crown in order to sample only needles developed on sunlit branches. One thousand needles were sampled from at least five randomly-selected trees of dominant species in each pine and spruce ICP stand where litterfall was also measured (Appendix 1). This enabled us to compare site- and species-specific mean mass of the oldest green needles with mean mass of 1000 or 100 needles collected in litterfall in subsequent years. For the comparison between green canopy needles and brown litterfall needles, we used two-year-old green needles sampled only in 2007. Such needles were assumed to be part of brown needles found in litterfall during the years 2008–2010 for spruce and during the years 2008–2009 for pine. Needles were transported to the laboratory (green immediately after the sampling, brown after emptying the litter traps), dried at 105 °C, and weighed to the nearest 0.1 mg.

Resorption associated with birch leaf senescence

Green leaves were sampled from two ICP stands where birch was dominant and litterfall was measured (Appendix 1) following Rautio *et al.* (2010). Green leaves were sampled every second year between 1995 and 2009. Mean mass of 100 sampled leaves from the canopy was compared with the mean mass of 100 brown leaves of litterfall of each sampling year.

Due to the large inter-annual variation in resorption of birch leaves in the two stands (one in south and one in north), we used only mean value for comparison with litter-biomass ratios. For pine and spruce resorption we had data from 14 stands, but only for one year for two year old needles. Therefore, also for pine and spruce we used the mean resorption value. The foliar weight loss before abscission among three main species in Finland was largest for birch (Table 3).

Results

Comparison between litterfall-biomass and needle-cohort turnover rates

The litterfall-biomass turnover rates (LT) of the pine and spruce plots with measured litterfall deviated in the upper range of the values from the needle-cohort turnover rates (NT) estimated by the kriging model for the same locations and corrected for resorption (Fig. 7). The NT values which were not corrected for resorption agreed better with LT values than the corrected ones. The agreement between NT and LT values was better for spruce than for pine. Spruce in northern Finland showed the strongest LT and NT agreement, whereas pine in the south showed the weakest agreement or rather a disagreement. Spruce canopies in the north contained the greatest numbers of needle cohorts, whereas pine canopies in the south contained the fewest. The average NT estimate across all spruce plots reached only 65% of the LT estimate when biomasses were estimated by the model outlined by Repola (2009) and only 58% when they were estimated with the Marklund (1988) model. The pine average NT was ~50% of the LT estimate for both models. The spruce site ICP_23 and pine site ICP_13 showed the largest LT as a result of the exceptionally large annual litterfall (Fig. 2 and Appendix 1).

Litterfall-biomass turnover rates

The LT estimates for stands dominated by Scots pine showed significant decline with increasing N coordinate (one-way ANOVA: $F_{1,14} = 43.6$, $p < 0.001$) irrespective of which foliar biomass model (Marklund or Repola) was used (Fig. 8). A statistically significant change with N coordinate was also found for the ratio between pine needle litterfall and stand basal area (one-way ANOVA: $F_{1,14} = 11, p < 0.001$).

For pine, the site LT means calculated with two Marklund models T18 and T19 were not

Table 3. The mean mass loss proportion between green foliage and brown foliar litterfall for tree species derived from the ICP intensive forest sites in Finland.

Tree species	Weight loss (%)	Number of plots
Scots pine	28	7
Norway spruce	34	8
Silver and downy birch	44	2

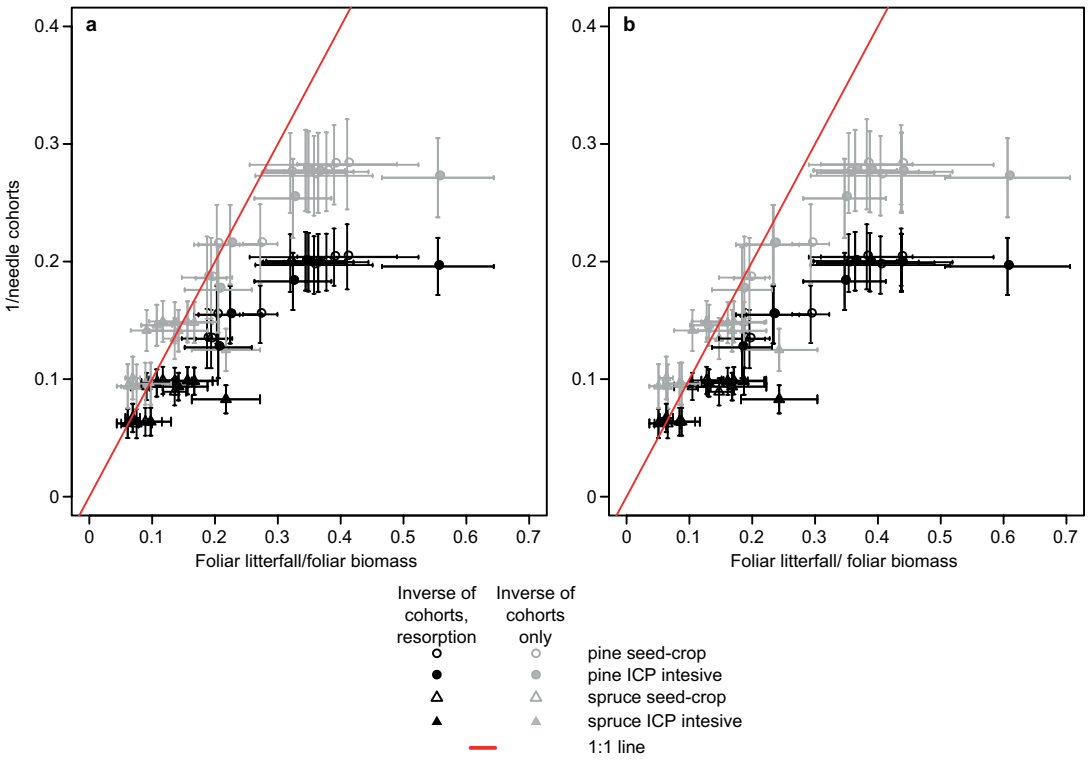

Fig. 7. Foliar turnover rates estimated from the litterfall-biomass ratio (LT) and from the inverse of the number of needle cohorts (NT) corrected (black symbols) or uncorrected (gray symbols) for mass loss during resorption. Foliar biomass for the litterfall-biomass ratio was estimated with equations (**a**) A4 and A10 of Repola (2009) or (**b**) T19 and G17 of Marklund (1988). The Repola model is based on the diameter and crown ratio, while the Marklund model is based on diameter, height, crown length and N coordinate. Dots represent comparison between individual ICP-intensive forest sites and seed-crop sites with measured litterfall data and the needle-cohort turnover rates estimated by the spatial kriging model for the same locations (grid). The error bars show the standard deviation. The standard deviation of litterfall-biomass ratio is based on the annual variation of litterfall. The standard deviation of the inverse of the number of needle cohorts is based on the spatial variance of the number of needle cohorts' estimate.

statistically different from the site LT means produced by the Repola model A4 (Fig. 8a). The relative slopes of fits between LT estimates and N coordinate of different models were found to be in the range from –0.89 to –0.96. The linear regressions with N coordinate explained 53%–55% of the variance in pine LT values (Fig. 8a).

The average LT of Norway spruce sites also declined with N coordinate ($F_{1,12}$ = 11.2, p = 0.006 for Marklund G17, and $F_{1,12}$ = 6.4, p = 0.026 for Repola A10), and differences between the relative slopes of linear fits, depending on which model was used, were small (from –0.78 to –1.0; *see* Fig. 8b). The linear regressions with N coordinate explained 27%–37% of the variation in LT (Fig. 8b). The decline in the ratio between the measured needle litterfall and stand basal area from the south to the north indicated that similar latitudinal decline in litterfall-biomass ratio turnover rates was not an artefact of the biomass models.

The birch LT values were affected by missing crown length measurements and the applied foliar biomass model (Fig. 8c). The LT site averages estimated with Eq. 2, which is a model using two basic tree variables (diameter and height), were scattered more (Fig. 8c). The two-variable biomass model gave the LT values > 1 for the southern and < 0.5 for the northern birch stands, respectively, which suggested modelling bias i.e. biomass overestimation in the north (Fig. 8c). The ratio between foliar litterfall and stand basal area declined from the south to the north (Fig. 8), which was not accounted

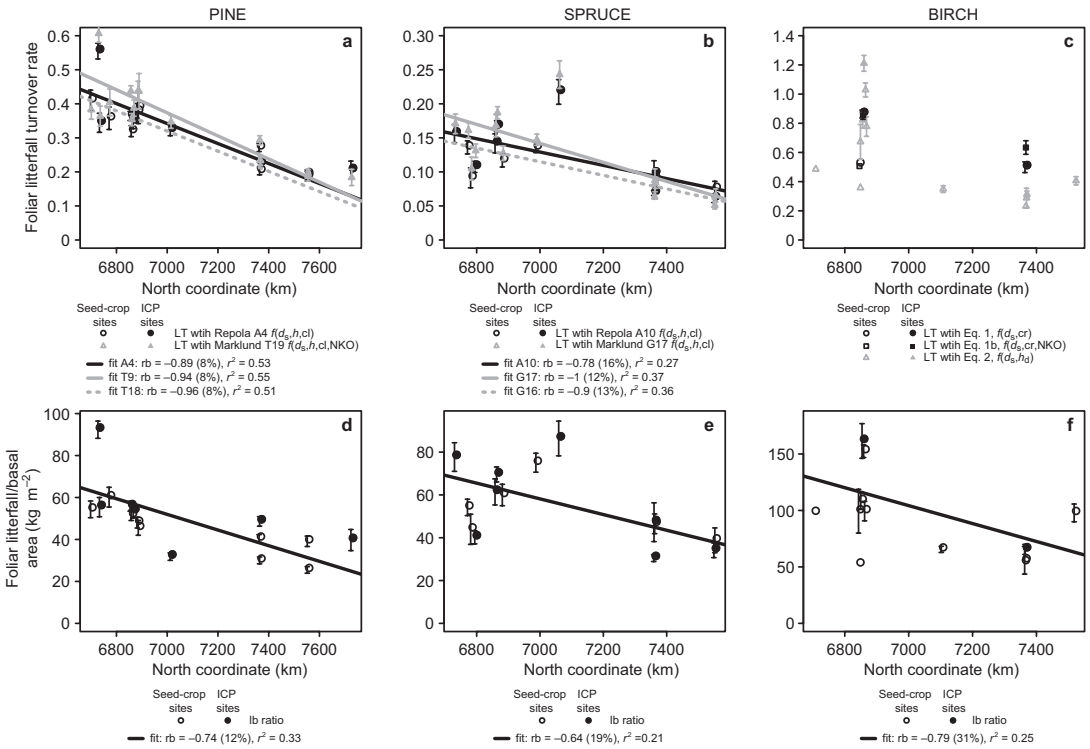

Fig. 8. (**a**–**c**) Decline in pine, spruce and birch foliar turnover rates (litterfall-biomass ratios, LT) with increasing N coordinate. (**d**–**f**) Decline in pine, spruce and birch ratios between measured litterfall and measured basal area with increasing N coordinate. Dots represent individual sites with measured litterfall data (open symbols for seed-crop and full symbols for ICP data). The error bars show the standard error for the annual variation in litterfall. Fitted lines show the effect of using different models. Fits are weighted by the number of annual litterfall at each site. The rb value shows the relative slope times 1000, which is the slope of the fit divided by the mean modelled foliar biomass, or mean basal area. The coefficients of variation of the relative slopes are shown in parentheses. Repola's models (Repola 2009) A4 and A10 are the functions of tree-stump diameter (d_s), height (h), and crown length (cl) (Appendix 2). Marklund's model (Marklund 1988) T19 is a function of d_s, h, cl, and N coordinate (NKO); G17 is a function of d_s, h, and cl; and T18 and G16 are the functions of d_s, and h (Appendix 2). The LT points behind the fits T18 and G16 are not shown. Our birch models are the functions of d_s, and crown ratio (cr), (Eq. 1a); and d_s, cr, and NKO (Eq. 1b), or, as in Eq. 2, function of d_s, and slenderness (h_d).

for in the two-variable LT models, confirming the foliar overestimation. However, including N coordinate in the foliar model failed to improve it, nor to produce reasonable LT estimates (data not shown).

Including N coordinate in the birch foliar model (Eq. 1b) using three basic tree variables (diameter, height, and crown length), produced reasonable LT estimates (Fig. 8). It gave estimates for both south and north that were close to the values estimated from the weight loss coefficient determined from resorption associated with leaf senescence. The estimated LT values in the north of around 0.5 (Eq. 1a, model without N coordinate) and 0.7 (Eq. 1b, model with N coordinate) for birch indicated that between 50% and 70% of the leaf mass remained after resorption. The mass comparison between brown and green leaves from the two ICP birch plots showed on average 56% of leaf mass remaining after resorption or 44% weight loss.

Needle-cohort turnover rates

As expected, the spatial variation in the NT measurements (plots) was in accordance with the spatial variation of the modelled NT values (*see* Fig. 9). The estimates of the foliar needle-cohort turnover rates (NT) for Scots pine (Fig. 9a) cor-

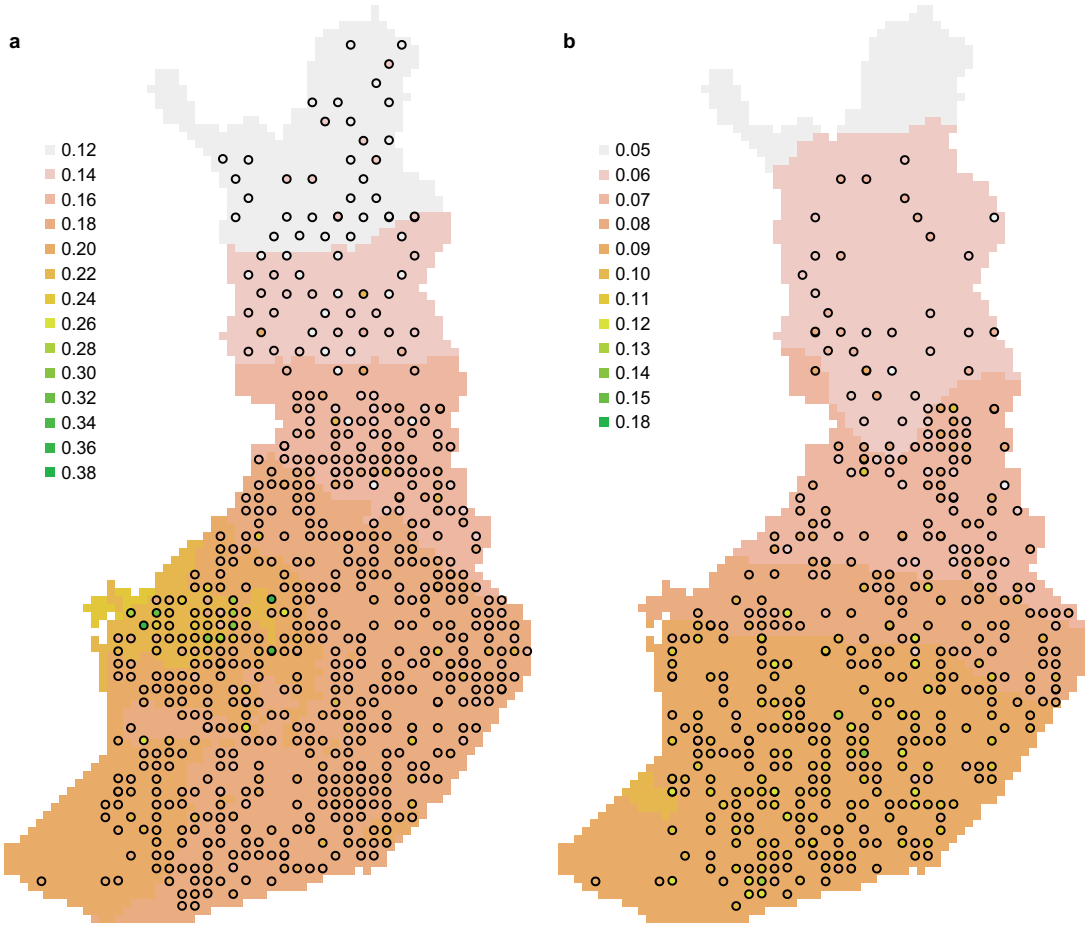

Fig. 9. Foliar litterfall turnover rates for (**a**) Scots pine and (**b**) Norway spruce derived as the inverse of the number of needle cohorts corrected for resorption (NT). Circles are the site-level NT for each ICP extensive monitoring plot overlaid on top of the spatial estimate of NT modelled by the universal kriging model in Finland. To download estimated number of foliar litterfall turnover rates for the grid based maps visit www.metla.fi/ghg/improving-soil-carbon-estimation.htm.

rected for the effect of nutrient resorption ranged from 0.38 to 0.12. The kriging model NT estimates were greater than 0.3 only for the limited area in the southwest. The prevailing NT level in the south was around 0.2, gradually declining to 0.15 in the middle of Finland and to 0.12 in the north. The NT values between individual sites and the spatial estimates agreed better in the south then in the north.

The measured NT values for Norway spruce (Fig. 9b) ranged from 0.18 to 0.05; only in one case was NT > 0.15. The modelled NT levels decreased from the average level of 0.11 in southern Finland to around 0.08 in central Finland, and to 0.06 in northern Finland. Turnover rates at about a dozen spruce sites in southern Finland were low (NT < 0.09).

Discussion

Foliar litterfall-biomass (LT) and needle-cohort (NT) turnover rates

Our foliar turnover rate estimates for evergreens were in the range of values reported for a similar climate (e.g. Ågren *et al*. 2007, Komarov *et al*. 2003, Muukkonen and Lehtonen 2004, Muukkonen 2005). Our study showed not only a decrease of foliage turnover rates towards the

north, as previously reported by Ågren *et al.* (2007), but also east–west variation (Fig. 9). While the needle-cohort (NT) rates well depicted spatial variation, overall they were lower than litterfall-biomass (LT) rates. The litterfall-biomass turnover rates (LT) of evergreens and the needle-cohort turnover rates (NT) differed mainly for Scots pine in southern Finland (Fig. 7).

During the last decade, spruce and in particular pine stands showed intensified defoliation in southern Finland (Nevalainen and Lindgren 2013). The reasons for this are unknown. It has been suggested that the increased defoliation in southern Finland may be linked with the corresponding increase in mean annual temperature (Tietäväinen *et al.* 2010). The number of needles in cohorts also tends to decrease in older stands after canopy closure (Jalkanen 1998), and needle litterfall tends to decrease with stand age (Albrektson 1988). However, we studied the needle cohort sets of the same ICP stands as Nevalainen and Lindgren (2013), and the pine stands in the south were relatively young, with a mean age of 57 years. Rather than intensified defoliation on the large scale, the young age of ICP stands may partly explain the difference between NT and LT estimates for evergreens. The stands with litterfall measurements were twice as old as the stands with needle cohorts. If the older stands had been shedding more needles from multiple cohorts simultaneously than younger trees, LT would have been greater than NT. Numerous stand, environmental, and weather factors can drive multi-cohort needle shedding (Jalkanen 1998). Also winter and storm breakage of shoots has been found to occasionally drive the interannual variation in pine-needle litterfall (Portillo-Estrada *et al.* 2013). However, our study focused on the long-term litterfall production level and the factors causing interannual variation in litterfall were assumed to level out in the course of several years (as in most of our plots) (Appendix 1).

The disagreement between pine NT and LT estimates in the south could also indicate the sensitivity of needle cohort-based estimates to quality of data (the number of measured needle cohorts and the weight loss coefficient). Visual evaluation of the number of needle cohorts in the canopy is prone to larger observational error at southern sites where the needle cohort quantities were lowest (Fig. 5). Typically, the leaf lifespan for evergreens increases with decreasing mean annual temperature (Van Ommen Kloeke *et al.* 2011). Earlier studies of the survival of pine needles in southern Finland (south of 62°4´N) give a mean needle age of 2.5 years (Muukkonen 2005). However, our ICP forest data showed a mean needle age of 3.9 years for the region south of 62°4´N. According to the METLA manual for the assessment of forest vitality (Nevalainen *et al.* 2010b), the needle cohort was counted as a whole, even if the proportion of shed needles reached 50%. The number of needle cohorts and especially the 50% threshold of cohort defoliation are difficult to measure precisely using binocular observations in the field. The larger number of cohorts could also be an indicator of a systematic bias due to differences in needle longevity between the sunlit and shaded crowns (Niinemets 1997), which may be more expressed in a dense canopy. Counting cohorts with only few remaining needles or cohorts of shaded crowns would lead to cohort overestimation, and thus underestimation of the cohort-based turnover rates. This would be avoided, if defoliation of needle cohorts could be measured more accurately than by visual estimation e.g. by calibrating the noise levels of 3D point clouds around coniferous branches from the hyper-spectral laser scanning signal (Hakala *et al.* 2012). Another source of error may arise if our weight loss coefficients averaged for the whole country changed with latitude. Needle mass resorption is known to vary with climate and soil fertility (Nordell and Karlsson 1995, Helmisaari 1992). Resorption correction based on live and fallen needles may also overestimate mass loss since a fraction of the annual litterfall was composed of live needles. Resorption clearly needs to be better resolved by more mass loss measurements and by improved understanding of allocation of nutrients and carbohydrates.

The LT estimates were prone to uncertainties, mainly due to the foliar biomass models, but also due to measurements of foliar litterfall. Foliar litterfall is subjected to weight loss through leaching (Ukonmaanaho and Starr 2001) and partial decomposition in littertraps during longer collection intervals. Additionally, wind speed plays

a major role in litterfall collection (Staelens *et al*. 2003, Portillo-Estrada *et al*. 2013). At sites with sparser canopies, litterfall may be underestimated due to higher wind velocities. Underestimated litterfall in general increases the LT estimate. The other side of the coin is that the models slightly underestimated foliar biomass, which also increased the LT values. In boreal forest, the foliage of coniferous trees peaks after the full leaf development typically around mid-summer to early June, and declines in autumn (Serbin *et al*. 2013). Trees in biomass studies (Repola 2008, Repola 2009, Marklund 1988) were harvested in autumn and part of the total foliage was already shed during the period between the leaf development and harvesting. For example, when we added the stand-specific litterfall of July and August (even without increasing the mass by the weight loss coefficient) to the total modelled foliar biomass of the stand, the stand foliage increased on average by 8.3% for pine and 1.2% for spruce, whereas the LT values decreased by 8.3% and 1.3%, respectively. Increasing the modelled biomass by accounting for the summer leaf fall from the canopy decreased LT estimates and increased the agreement between the NT and LT levels for evergreens.

The lack of crown length in Marklund's pine and spruce models caused a systematic increase in modelled foliar biomass and a reduction of the LT (Fig. 8). However, the difference in LT values between two Marklund models (with and without the crown length) was not statistically significant. Similarly, the difference in LT values between Marklund's and Repola's models (when both included the crown length) was not statistically significant. This suggested that the pine and spruce trees in Marklund's (1988) study, which were harvested earlier in autumn, did not have significantly larger foliar biomass than the trees of Repola's (2009) study, which were harvested later in autumn.

Foliar litterfall-biomass turnover rates for birch

The biomass models for estimating LT values for birch that used tree diameter and height alone performed well in the south but overestimated biomass in northern latitudes. When N coordinate was added to the model with diameter and crown length, then LT values decreased less from south to north than in the models without N coordinate (Fig. 8). However, crown length was measured only in few stands. The birch stands with litterfall series from the 1960s lack the measurements of tree crown length (Appendix 1). The weight loss coefficients of data from ICP_32 and ICP_33 suggested that the LT level was reasonable. The weight loss of birch leaves was on average 44% (Table 3), with a greater value in the northern than southern site. Our birch weight-loss coefficient is at the upper limit of the reported values from northern Sweden, and about a double of the reported average weight-loss coefficient (Nordell and Karlsson 1995, Viro 1955). However, in the study by Nordell and Karlsson (1995), yellow leaves were still hanging on the trees when collected. In our study, we compared green leaves with yellow leaves collected into the litter collectors. Our leaf litter expressed the mass, which did not include the nutrients and carbohydrates resorbed prior to abscission, and which was also potentially reduced by nutrients leaching from the litter collectors (Ukonmaanaho and Starr 2001). The rapidly decomposable carbohydrates were probably lost during this period. On the other hand, the foliar biomass models in our study probably underestimated the foliage as the sample trees were harvested in late summer with lower than maximum foliage (Rautiainen *et al*. 2009) (Parviainen 1999, Ilomäki *et al* 2003, Repola *et al* 2008). Thus, adding the birch stand-specific litterfall of July and August (without increasing the mass by the weight loss coefficient) to the total modelled leaf biomass of the stand, increased the foliage on average by 5.1%, whereas the LT values decreased by 7.7%.

Foliar turnover rates used in Finnish greenhouse gas inventory model

Our foliar litterfall-biomass turnover rates (LT) and needle-cohort turnover rates (NT) differed from the turnover rates used in the Finnish greenhouse gas (GHG) inventory model for evergreens (0.1 and 0.05 for spruce in north and south, 0.245 and 0.154 for pine, respectively),

and deciduous (0.79 for the whole of Finland) (Finland's National Inventory Report 2013) (Figs. 7 and 8).

For deciduous forests that are represented by birch, the existing data are not sufficient to justify the inclusion of foliar turnover rates in the GHG inventory. Allometric relations between the foliage mass and diameter, height, and crown length are needed from more trees than are currently available in order to build reliable birch biomass models especially for northern Finland. For deciduous trees, the current GHG inventory turnover rates are based on a ratio between leaf mass before and after the yellowing process in the autumn. The spatial variation of the foliar weight loss or nutrient resorption ratio before abscission needs further research both for deciduous and for evergreens.

For evergreens, GHG inventory turnover rates have limited spatial variability and seem to underestimate foliar turnover rates as compared with our LT estimates (Fig. 8). For evergreens, the inventory foliar turnover rates are based on an inverse of the number of needle cohorts. The GHG inventory values are therefore closer to our NT estimates. However, since the number of needle cohorts based on visual evaluation of ICP extensive forest was possibly overestimated and that the estimated mass loss of needles before abscission lacked spatial precision, the NT method underestimates the foliar litter production. In order to improve the spatial distribution of turnover rates, we suggest using the inverse values from the map of cohort sets (Fig. 5). The simple inverse of cohort numbers agreed somewhat better with our LT estimates (Fig. 7) than the inverse of the number of needle cohorts corrected for resorption (NT). The use of poorly-resolved resorption correction factor of NT indeed needs further improvement. However, the advantage of using our spatial variation of NT estimates that is based on extensive measurements is clear, and the use of an artificial correction factor could thus be avoided. Further improvement for precise NT estimates would require data on the total needle biomass distribution among needle cohorts or defoliation of cohorts (in addition to the currently measured number of needle cohorts) and data on spatial variation of needle mass loss before abscission.

Conclusions

We estimated crucial parameters of greenhouse gas inventories; foliar turnover rates of Scots pine, Norway spruce and silver and downy birch stands distributed all over Finland. For evergreens, we compared the foliar turnover rates based on two methods: the inverse of the number of needle cohorts corrected or uncorrected for mass loss due to resorption (NT), and the ratio between measurements of litterfall and modelled foliar biomass (LT). For deciduous, we only determined foliar turnover rates based on the litterfall-biomass ratio. Our data were extensive long-term measurements from plots across Finland. One method was based on the visual canopy evaluation, and sampling and measurement of live and litterfall leaf mass. The other method was based on the measurements of foliar litterfall and on foliar biomass models built from measurements of harvested living foliage.

The NT and LT methods had their pros and cons. Pros of the NT method were the detailed spatial estimates of turnover rates throughout the country, and that needle cohort data could be more rapidly acquired; whereas the cons were the inability to capture exceptional multiple cohort defoliation, limited precision of visual evaluation, and poor data on spatio-temporal variations in mass resorption prior to needle abscission. Pros of the LT method were the precise long-term measurements of the litterfall on multiple sites distributed across Finland, the ability to capture exceptional short-term defoliation, and the applicability of the method for both evergreens and deciduous; whereas the cons were the uncertainty of modelled foliar biomass, and the greater time and effort needed to acquire foliar litterfall data. Sole use of the NT method can lead to underestimation of litterfall input under the present conditions of increased defoliation of Scots pine in southern Finland (Nevalainen and Lindgren 2013). Sole use of the LT method can lead to spatially-biased results when applying averaged turnover rates for the whole country. Therefore, we suggest a combination of the two methods. One way of combining the two sources would be, for instance, to develop a litterfall-model based on the basic tree dimensions, needle cohorts, litterfall, and cli-

mate conditions. The other possibility to use the needle-cohort method more precisely would be to acquire data on defoliation of needle cohorts (needle densities) in addition to recording the number of needle cohorts.

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Appendix 1. Scots pine, Norway spruce, silver and downy birch stand characteristics from ICP intensive (ICP_xx) and seed-crop plots (codes other than ICP_xx). The spatial position of each stand is given as N and E coordinates (km) in Finnish KKJ-3 (YKJ) coordinate system. Tree diameter, height, and crown ratio, and annual litterfall are the stand means for the period of corresponding annual litterfall and tree measurements (data period).

Species	Stand Id	N coord. (km)	E coord. (km)	Data period	Diameter at 1.3 m (cm)	Height (m)	Crown ratio	Basal area (m^2 ha^{-1})	Foliar litterfall (kg m^{-2} y^{-1})
Scots pine	ECK1	6698.290	3088.260	1991–1991	23.19	16.45	0.38	26.69	0.138
	ICP_13	6726.988	3327.118	1999–2010	22.22	20.59	0.40	22.87	0.193
	ICP_18	6732.573	3546.242	2005–2005	23.46	19.45	0.42	19.71	0.121
	AUL29	6770.580	3362.720	1995–2003	21.25	20.59	0.41	20.26	0.116
	ICP_16	6854.033	3623.352	2004–2009	22.12	23.10	0.35	28.11	0.143
	PUN45	6858.120	3622.120	1990–2001	33.23	23.23	0.48	23.00	0.117
	ICP_10	6865.605	3353.490	2004–2010	25.21	21.63	0.40	21.88	0.100
	KUO23	6881.710	3385.210	1991–2002	35.44	26.82	0.38	23.26	0.106
	VIL2A	6886.500	3368.470	1992–2002	35.75	25.89	0.37	23.85	0.117
	ICP_20	7011.694	3686.828	1999–2009	23.87	17.81	0.32	25.83	0.085
	ROI29	7361.950	3484.050	1991–1991	33.25	20.51	0.48	15.68	0.059
	ICP_6	7363.505	3488.068	1999–2009	13.55	12.73	0.54	20.39	0.096
	ROI27	7363.630	3488.250	1991–2001	29.06	21.70	0.42	24.64	0.072
	KIT2	7551.710	3379.880	2002–2002	26.65	16.88	0.38	22.50	0.070
	ICP_1	7723.832	3573.924	2009–2009	20.78	11.15	0.58	13.33	0.072
Norway spruce	ICP_12	6730.421	3325.488	1999–2004	24.49	21.32	0.69	24.53	0.231
	AUL27	6771.110	3362.580	1990–1995	46.98	33.42	0.70	40.05	0.197
	HE565	6781.210	3448.540	1991–1991	36.06	28.47	0.74	32.84	0.176
	ICP_19	6794.205	3396.330	1999–2009	24.13	21.09	0.55	35.20	0.148
	ICP_17	6858.461	3622.424	1999–2009	33.51	27.62	0.65	34.10	0.192
	ICP_11	6863.456	3358.539	1999–2004	22.80	20.68	0.59	33.91	0.267
	KUO35	6881.070	3384.680	1991–1991	23.16	20.63	0.70	26.38	0.193
	SI544	6986.770	3537.610	1990–1990	28.67	23.72	0.78	21.98	0.143
	ICP_23	7059.249	3276.050	1999–2009	22.32	20.74	0.56	35.69	0.284
	ICP_21	7359.001	3612.225	2000–2009	10.18	8.58	0.64	10.32	0.032
	ICP_5	7360.120	3484.094	2009–2009	14.86	11.80	0.72	18.72	0.122
	ROI18	7361.920	3484.770	1991–2001	20.35	15.74	0.76	20.77	0.124
	ICP_3	7548.603	3384.447	2004–2009	12.75	8.88	0.83	14.46	0.057
Silver and downy birch	HAM3	6703.144	3097.989	1963–1963	16.08	15.41		13.49	0.132
	NOO89	6843.010	3232.890	2000–2001	18.85	20.37	0.43	42.70	0.233
	NOO210	6843.400	3231.100	1990–2001	16.78	19.07		12.21	0.121
	HAR571	6850.284	3441.811	1961–1969	27.21	25.16		13.84	0.146
	ICP_33	6854.033	3623.352	2004–2010	13.21	17.33	0.63	16.41	0.239
	PUN54	6858.806	3621.140	1961–1969	25.10	22.51		11.58	0.171
	KER543	6861.544	3624.909	1967–1969	22.95	23.89		14.04	0.143
	KAJ548	7101.532	3535.462	1961–1970	16.96	16.56		13.81	0.092
	ROI28	7361.160	3486.038	1970–1971	9.69	10.69		10.54	0.038
	ROI21	7362.634	3488.956	1961–1971	20.07	17.50		8.65	0.049
	ICP_32	7363.505	3488.068	2005–2010	16.69	15.60	0.52	18.48	0.122
	KIT1B	7518.305	3408.510	1961–1965	15.96	13.92		7.47	0.068

Appendix 2. Functions and their parameters used to model foliage for Scots pine and Norway spruce.

Repola's (2009) foliar biomass function for pine needles A4:

$$\ln\left(y_{k,i}\right) = -1.748 + 14.824\frac{d_{\mathrm{Sk},i}}{\left(d_{\mathrm{Sk},i}+4\right)} - 12.684\frac{d_{k,i}}{\left(d_{k,i}+1\right)} + 1.209\ln\left(\mathrm{cl}_{k,i}\right) + \left(\frac{0.032+0.093}{2}\right),$$

where $y_{k,i}$ is the foliar biomass (kg m^{-2} y^{-1}) of kth stand and ith tree, $d_{\mathrm{sk},i}$ (cm) is stump diameter which is transformed breast height diameter (D_{13}) [d_s (cm) = $1.25D_{13}$ + 2, (Laasasenaho (1982) as cited in Repola (2008)], $h_{k,i}$ (m) is tree height, and $\mathrm{cl}_{k,i}$ (m) is crown length.

Repola's (2009) foliar biomass functions for spruce needles A10:

$$\ln\left(y_{k,i}\right) = -0.085 + 15.222\frac{d_{\mathrm{Sk},i}}{\left(d_{\mathrm{Sk},i}+4\right)} - 14.446\frac{h_{k,i}}{\left(h_{k,i}+1\right)} + 1.273\ln\left(\mathrm{cl}_{k,i}\right) + \left(\frac{0.028+0.087}{2}\right),$$

where $d_{\mathrm{sk},i}$, $h_{k,i}$, and $\mathrm{cl}_{k,i}$ are same as in eq. A4.

Marklund's (1988) foliar biomass function for pine needles T18:

$$\ln\left(y_{k,i}\right) = -3.47 + 12.1095\frac{d_{k,i}}{\left(d_{k,i}+7\right)} - 1.565\ln\left(h_{k,i}\right) + 0.0413h_{k,i},$$

where $y_{k,i}$ is the foliar biomass (kg m^{-2} y^{-1}) of kth stand and ith tree, $d_{\mathrm{sk},i}$ (cm) is breast height diameter, and $h_{k,i}$ (m) is tree height.

Marklund's (1988) foliar biomass function for pine needles T19:

$$\ln\left(y_{k,i}\right) = -2.6024 + 9.8471\frac{d_{k,i}}{\left(d_{k,i}+7\right)} - 1.6717\ln\left(h_{k,i}\right) + 0.026h_{k,i} - 1.0419\ln\left(\mathrm{cl}_{k,i}\right) - 0.0123\mathrm{NKO}_{k,i},$$

where $y_{k,i}$ is the foliar biomass (kg m^{-2} y^{-1}) of kth stand and ith tree, $d_{k,i}$ (cm) is breast height diameter, $h_{k,i}$ (m) is tree height, and $\mathrm{cl}_{k,i}$ (m) is crown length and $\mathrm{NKO}_{k,i}$(100 km) is N coordinate.

Marklund's (1988) foliar biomass function for spruce needles G16:

$$\ln\left(y_{k,i}\right) = -1.8551 + 9.7809\frac{d_{k,i}}{\left(d_{k,i}+12\right)} - 0.4873\ln\left(h_{k,i}\right)$$

where $d_{k,i}$, and $h_{k,i}$ are same as in the explanations to the function T18.

Marklund's (1988) foliar biomass function for spruce needles G17:

$$\ln\left(y_{k,i}\right) = -1.5732 + 8.4127\frac{d_{k,i}}{\left(d_{k,i}+12\right)} - 1.5628\ln\left(h_{k,i}\right) + 1.4032\ln\left(\mathrm{cl}_{k,i}\right),$$

where $y_{k,i}$ is the foliar biomass (kg m^{-2} y^{-1}) of kth stand and ith tree, $d_{\mathrm{sk},i}$ (cm) is breast height diameter, and $h_{k,i}$ (m) is tree height, and $\mathrm{cl}_{k,i}$ (m) is crown length.

Appendix 3. Compiled tree measurements from three studies used for building birch foliage models. The spatial position of each tree is given as N and E coordinates (km) in the Finnish KKJ-3 (YKJ) coordinate system.

Study	E coord. (km)	N coord. (km)	Diameter (cm)		Height (m)		Foliage (kg)
			D_{13}	At crown base	H	At crown base	
Ilomäki *et al.* (2003)	3544.259	6917.027	23.4	20.7	18.55	3.67	7.707
—»—	3544.274	6917.027	20.2	16.9	17.86	5.69	7.153
—»—	3544.290	6917.027	17.7	16.2	18.13	4.37	4.968
—»—	3544.501	6917.001	16.0	11.6	17.34	8.60	2.894
—»—	3544.517	6917.002	14.7	10.4	17.02	7.82	2.230
—»—	3544.532	6917.002	14.6	9.7	17.32	9.07	2.043
—»—	3544.388	6916.967	13.8	8.2	18.65	10.67	1.342
—»—	3544.548	6917.002	12.0	8.7	16.33	8.08	1.312
—»—	3544.564	6917.002	11.0	8.6	15.46	6.84	1.244
—»—	3544.404	6916.967	11.2	7.0	17.65	10.35	0.798
—»—	3544.579	6917.002	6.0	4.2	9.80	4.23	0.297
—»—	3544.420	6916.967	9.4	4.9	16.71	11.44	0.590
—»—	3544.435	6916.968	8.3	4.2	15.43	10.43	0.390
—»—	3544.451	6916.968	7.6	2.8	14.61	11.45	0.230
—»—	3544.466	6916.968	6.1	3.0	12.00	7.97	0.157
—»—	3544.482	6916.968	7.8	4.5	15.60	10.50	0.421
—»—	3544.497	6916.968	7.9	3.8	15.95	11.35	0.426
—»—	3544.513	6916.969	5.7	2.5	11.90	8.80	0.121
Parviainen (1999)	3357.456	6863.884	7.2	6.9	8.25	1.60	1.491
—»—	3358.409	6862.756	2.4	3.1	3.35	0.52	0.216
—»—	3358.425	6862.755	4.1	5.2	5.53	0.77	0.703
—»—	3358.441	6862.754	1.8	2.7	3.27	0.40	0.135
—»—	3358.379	6863.566	36.6	30.3	27.82	9.70	14.654
—»—	3358.048	6864.085	24.9	17.9	22.85	9.40	3.585
—»—	3358.850	6863.682	17.4	14.0	17.44	6.39	4.076
—»—	3357.472	6863.883	9.6	8.9	9.23	1.65	2.346
—»—	3359.393	6864.007	10.9	7.7	11.60	4.60	1.417
—»—	3358.136	6863.490	7.5	6.6	7.80	1.65	0.940
—»—	3358.456	6862.754	1.6	2.5	3.03	0.42	0.133
—»—	3358.472	6862.753	0.5	0.5	1.80	0.42	0.040
Repola (2008)	3398.569	6807.339	16.4	13.6	17.40	6.30	7.003
—»—	3398.585	6807.339	14.1	11.2	17.30	8.90	1.789
—»—	3398.601	6807.338	19.5	16.4	19.60	7.90	3.917
—»—	3398.617	6807.338	19.1	15.6	19.60	6.60	4.903
—»—	3398.688	6807.306	18.8	15.1	21.40	8.10	3.439
—»—	3398.704	6807.306	13.2	10.9	20.20	9.90	1.800
—»—	3398.720	6807.305	15.0	12.0	19.80	9.10	2.673
—»—	3398.736	6807.305	16.5	14.3	21.30	12.10	2.110
—»—	3398.752	6807.304	11.8	9.4	19.70	11.70	1.070
—»—	3492.596	6900.361	17.3	15.1	21.50	9.30	4.976
—»—	3492.612	6900.361	24.3	19.9	22.70	10.80	4.527
—»—	3492.627	6900.361	26.1	19.0	23.10	7.80	6.271
—»—	3492.643	6900.361	20.2	17.1	23.50	10.40	3.317
—»—	3492.633	6900.364	16.9	15.1	22.50	13.30	2.518
—»—	3492.649	6900.364	21.6	18.2	23.70	9.50	6.100
—»—	3492.664	6900.364	22.9	18.3	20.30	8.30	6.957
—»—	3492.680	6900.364	19.1	15.2	21.90	10.30	3.528
—»—	3492.695	6900.364	12.2	10.4	19.60	11.70	1.337
—»—	3492.634	6900.297	17.0	15.3	21.90	12.30	3.164
—»—	3492.650	6900.297	21.7	18.9	22.50	10.20	6.797
—»—	3492.665	6900.297	24.3	19.2	23.90	11.60	6.770